Records of the Western Australian Museum **17**: 213–220 (1995).

Morphological variation in Bearded Tomb Bats (*Taphozous*) in Maluku Tenggara and Nusa Tenggara Timur, Indonesia

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Abstract – Bearded Tomb Bats, *Taphozous melanopogon* and *T. achates*, were recently collected on Wetar, Tanimbar and Kai Islands, eastern Indonesia.

Morphological comparisons of skull, dentary, dental and external characters and a univariate and multivariate statistical analyses of 138 specimens, indicated that the animals from Wetar Island were *T. a. achates*. Those from the Tanimbar and Kai Islands were morphologically distinct from both *T. melanopogon* and *T. a. achates*, but were closer to the latter taxon. They are herein described as a new subspecies of *T. achates*, *T. achates minor*.

INTRODUCTION

An earlier study of the morphological variation of Bearded Tomb Bats in Nusa Tenggara, Indonesia, by Kitchener *et al.* (1993a) recognised the occurrence in that region of two species, *Taphozous m. melanopogon* Temminck, 1841 and *T. achates* Thomas, 1915. The former was found on islands in the Inner Banda Arc (Lombok, Sumbawa, Moyo and Alor), as well as Timor in the Outer Banda Arc. Koopman and Gordon (1992) also report that a specimen of *T. melanopogon* exists in the American Museum of Natural History from Kei (= Kai) Island. *Taphozous achates* occurred only on islands in the Outer Banda Arc (Savu, Roti and Semau and possibly also on Timor).

Kitchener *et al.* (1993a) noted that while there was little morphological differentiation in *T. m. melanopogon* among islands in Nusa Tenggara, there appeared to be some differentiation among populations of *T. achates*. These authors suggest that *T. m. melanopogon* is Laurasian in origin and may be a relatively recent inhabitant of Nusa Tenggara and speculate that "*T. achates* alone will be found to occur on the smaller Gondwanic islands such as Leti, Babar, Tanimbar, Kei (= Kai) and Aru". The recent collection of Bearded Tomb Bats from Wetar, Tanimbar and Kai Islands by staff from the Western Australian Museum and Museum Zoologicum Bogoriense allows for this speculation to be examined.

Recent studies on morphological variation (and in some cases of genetic variation) have shown a tendency for some species of bats that are widely distributed in Nusa Tenggara and Maluku Tenggara to differentiate morphologically in the southeastern parts of these provinces, where the islands in the Inner and Outer Banda Arcs become more isolated from the other islands in these areas (Kitchener and Maryanto 1993; Kitchener *et al.* 1993b; 1995a,b).

This paper will describe the morphological variation of the Bearded Tomb Bats from the southern region of Maluku Tenggara and report on the taxonomic status of these bats.

MATERIAL AND METHODS

Measurements from 111 adult specimens used in the previous analysis of morphological variation in *Taphozous* in this region presented in Kitchener *et al.* (1993a) were combined with measurements from an additional 33 adult specimens from Wetar Island (9), Kai Besar Island (12) and Selaru Island, Tanimbar Group (12) for statistical analysis. The measurements recorded were the same as those documented in that previous study. However, palate length in both this and the previous study was measured from the posterior margin of the palate to the posterior margin of the anterior palatal incisor, and not to the anterior edge of the C^1 alveoli as figured in Kitchener *et al.* (1993a: figure 1).

The measurements were as follows: GSL, greatest skull length; IOW, least interorbital breadth; POW, postorbital breadth; CW, cranial breadth; MW, mastoid width; ZW, zygomatic width; PPL, post palatal length; PL, palatal length; DBC, distance between cochleae; BL, bulla length; GBPL, greatest basial pit length; DL, dentary length; C^1BW, C^1 basal breadth; C^1C^1B, width across C^1C^1 labial surfaces at alveoli; M^3M^3B, width across M^3M^3 labial surfaces at alveoli; C^1M^3L, maxillary tooth row length, from C^1alveoli anterior edge to M^3 alveoli posterior edge; M^2L, M^2 crown length; M^2W,

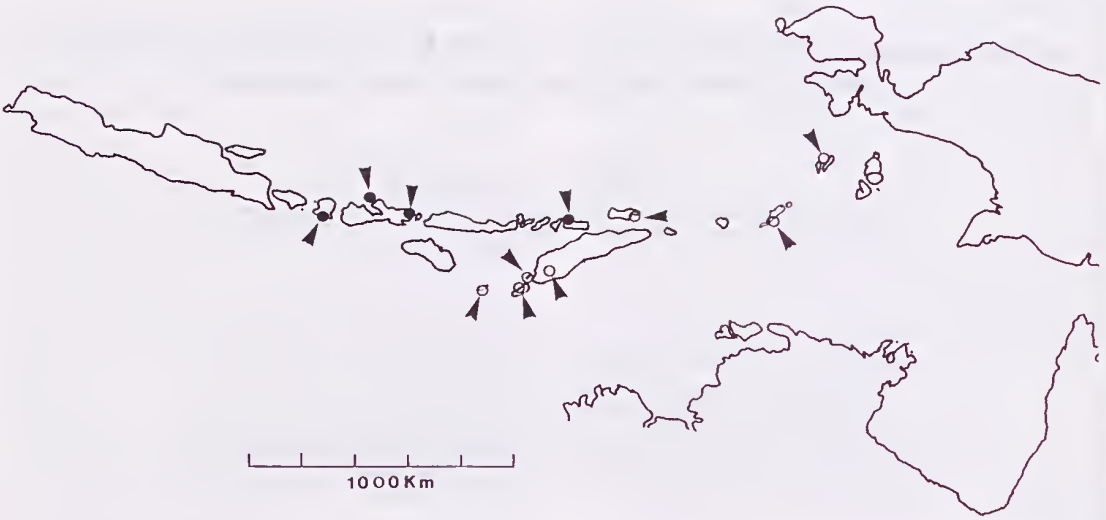

Figure 1 Locality of *Taphozous melanopogon* (●) and *T. achates* (O) used in this study.

M^2 crown breadth; SVL, tip of snout to anus length; TVL, distal tip of tail to anus length; EL, ear length; GTW, greatest tragus breadth; RL, radius length; D3–5MCL, digit 3–5 metacarpal length; D3P1–2L, digit 3 phalanx 1–2 length; TL, tibia length; PES, pes length.

All skull, dentary and dental characters were measured with vernier callipers to 0.01 mm and external measurements to 0.1 mm.

Adult status was recognised and adult age classes determined in the manner described in Kitchener *et al.* (1993a).

The effect of sex and island on all characters was examined by standard multiple regressions (where all effects were assessed simultaneously) for the islands which had both sexes and all age classes present (Lombok, Sumbawa, Timor, Roti, Wetar, Kai Besar and Selaru (Tanimbar Group). Graphical inspection of raw data using residual plots from regression analysis gave no indication of heteroscedasticity. Because of the number of interactions tested in this analysis the probability level was set at $P<0.01$.

Stepwise Canonical Variate (Discriminant Function) Analysis (DFA) were run for skull, dentary and dental characters and separately for external characters after first examining for sexual dimorphism or age effects. A reduced set of five of these characters was used in the presented DFA because they provided similar DF plots to the

Table 1 Measurements (in mm) for skull, dentary, dental and external body characters of adult *Taphozous a. achates* from Wetar Island and *T. a. minor* subsp. nov. from both Yamdena and Kai Besar Islands. $\bar{X}$, mean; SD, standard deviation; MIN, minimum; MAX, maximum and N, sample size.

		GSL	IOW	POW	CW	MW	ZW	PPL	PL	DBC	BL	GBPL	DL	C^1BW
T. a. achates	$\bar{X}$	21.66	6.35	4.72	10.00	11.38	13.25	10.36	6.24	2.31	5.02	4.01	17.21	1.29
(Wetar Island)	SD	0.39	0.23	0.08	0.19	0.17	0.25	0.19	0.19	0.14	0.14	0.14	0.30	0.07
	MIN	21.22	5.95	4.65	9.62	11.12	12.88	10.09	6.05	2.09	4.79	3.85	16.82	1.15
	MAX	22.55	6.59	4.89	10.25	11.62	13.71	10.67	6.52	2.51	5.13	4.34	17.76	1.37
	N	9	9	9	9	9	8	9	9	9	8	9	9	9
T. a. minor	$\bar{X}$	20.36	6.25	4.57	9.62	11.00	12.76	9.98	5.82	2.12	4.72	3.71	16.32	1.17
subsp. nov.	SD	0.21	0.29	0.09	0.09	0.10	0.17	0.13	0.17	0.06	0.09	0.11	0.25	0.07
(Yamdena Island)	MIN	19.94	5.82	4.48	9.42	10.88	12.42	9.82	5.43	2.04	4.57	3.49	12.96	1.06
	MAX	20.61	6.62	4.73	9.78	11.15	13.01	10.21	6.10	2.23	4.80	3.84	16.65	1.28
	N	12	12	12	12	12	12	12	12	12	8	12	12	12
T. a. minor	$\bar{X}$	20.74	6.21	4.65	9.64	11.09	12.97	10.10	6.02	2.15	4.74	3.85	16.56	1.26
subsp. nov.	SD	0.25	0.23	0.07	0.10	0.09	0.11	0.23	0.14	0.12	0.08	0.12	0.16	0.06
(Kai Besar Island)	MIN	20.43	5.91	4.54	9.42	10.96	12.81	9.75	5.77	2.01	4.61	3.56	16.27	1.20
	MAX	21.12	6.61	4.81	9.80	11.25	13.19	10.43	6.27	2.41	4.86	4.07	16.80	1.38
	N	12	12	12	12	12	12	12	12	12	12	12	12	12

larger set of characters. This reduced set of characters was selected because the sample size of the smallest island group was less than the total number of characters considered. This reduced set of characters was selected because they provide values that minimise Wilk's Lambda. All analyses used the statistical package SPSS PC+.

Univariate Statistics

The mean, standard deviation, and range of measurements of skull, dentary and dental characters of both adult male and adult female *Taphozous* from Wetar, Tanimbar and Kai Island are presented in Table 1. Comparable measurements for specimens from other islands in Nusa Tenggara are presented in Kitchener *et al.* (1993a: table 2). These measurements indicate that the Tanimbar and Kai individuals were of similar size but the Wetar individuals were generally larger in skull, dentary and dental measurements.

Multiple regression analysis

Skull, dentary and dental characters

This analysis examined the association between the main effects of sex, age and island and the recorded measurements and the interactions between these effects.

Sex and age

There were no significant interactions between these effects and no significant association between these measurements and age and sex, except for M^2 width and age ($F_{2,82}$=5.821; p=0.004).

Island

All characters were significantly associated with island at P<0.001, except for postorbital width (P=0.013).

Externals

Sex and age

There were no significant associations between sex and age and the external characters. There was, however a significant interaction for tail to vent length between sex and island ($F_{6,88}$=3.863; P=0.002).

Island

Only snout to vent length, greatest tragus breadth, digit 4 metacarpal length, digit 5 metacarpal length and pes length were not significantly associated with island; tail to vent length was the most significantly associated variable ($F_{6,88}$=10.699; P=<0.001).

Discriminant function analysis (DFA)

Skull, dentary and dental characters

Because of the absence of significant sexual dimorphism and the significant association of only one character (M^2 width) with age, the DFA based on skull, dentary and dental characters and the 11 island populations (Lombok, Sumbawa, Moyo, Alor, Wetar, Savu, Roti, Semau, Timor, Tanimbar and Kai Besar) was run for males and females combined, and all characters (17), except M^2 width.

A DFA run with a reduced set of five characters (dentary length, greatest basial pit length, bulla length, M^2 length and interorbital breadth) and three island groups [the Lombok Group (Lombok, Sumbawa, Moyo, Alor and Timor); the Savu Group (Savu, Roti, Semau and Wetar); and the Tanimbar

Table 1 (continued)

C^1C_1B	M^3M^3B	C^1M^3L	M^2L	M^2W	SVL	TVL	EL	GTW	RL	D3MCL	D3P1L	D3P2L	D4MCL	D5MCL	TL	PES
4.24	9.12	9.35	2.15	2.43	70.6	27.7	21.5	5.1	64.5	57.8	20.3	22.9	46.3	36.7	25.8	11.6
0.15	0.27	0.22	0.08	0.09	3.1	2.1	1.1	0.2	0.8	1.1	0.7	0.9	1.1	0.7	0.6	0.4
3.98	8.70	9.06	2.07	2.28	64.9	23.4	19.8	4.9	63.2	55.5	19.6	21.1	44.4	35.5	24.5	11.2
4.55	9.62	9.74	2.28	2.61	74.9	30.3	23.1	5.4	65.4	58.9	21.2	24.2	48.2	37.4	26.5	12.2
9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9
3.99	8.77	8.63	1.97	2.32	69.6	26.8	19.1	4.7	62.5	54.9	20.1	21.9	44.4	34.8	24.3	11.4
0.07	0.14	0.15	0.06	0.07	3.0	1.7	0.5	0.2	1.1	0.8	0.5	0.4	1.0	0.7	0.4	0.3
3.90	8.59	8.45	1.83	2.14	65.3	24.0	18.3	4.4	60.2	53.3	19.5	21.3	43.0	34.0	23.8	10.7
4.09	8.95	8.89	2.06	2.41	75.2	30.8	19.7	5.1	64.1	56.0	20.8	22.8	45.9	35.9	24.9	11.9
12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12
4.15	8.95	8.91	1.96	2.29	73.5	26.6	20.3	5.0	61.2	54.6	19.6	21.2	44.3	34.3	24.6	11.4
0.06	0.12	0.17	0.08	0.08	3.7	1.3	0.4	0.2	0.8	0.6	0.4	0.6	0.7	0.6	0.4	0.2
4.03	8.65	8.63	1.79	2.20	65.2	23.8	19.8	4.7	59.5	53.8	19.1	19.8	43.0	33.1	23.9	11.0
4.29	9.09	9.12	2.05	2.41	79.7	28.2	20.9	5.2	62.5	55.5	20.5	22.1	45.1	35.4	25.3	11.8
12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12

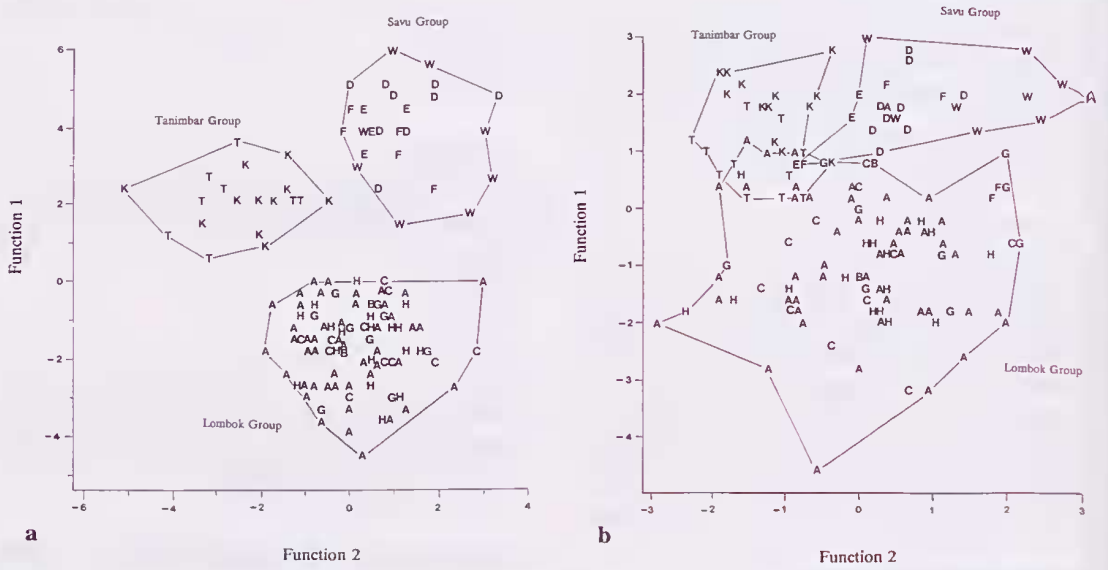

Figure 2 Canonical variate analysis for both adult male and adult female Bearded Tomb Bats based three island groups (Tanimbar Group; Savu Group, and Lombok Group). The plots of Functions 1 and 2 were based on (a) five selected skull, dentary and dental characters and (b) five selected external characters. The island codes within these three groups were as follows: A, Lombok; B, Alor, C, Timor; D, Roti, E, Savu; F, Semau; G, Moyo; H, Sumbawa; W, Wetar; K, Kai and T, Tanimbar.

Group (Yamdena and Kai Besar)] produced a similar association of these island populations in Discriminant Function space to that produced by the above DFA using all islands and 17 characters. This latter DFA produced two significant Functions (Figure 2a). Function 1 explained 82.5% of the variance and Function 2, 17.5%. All individuals were correctly classified to their appropriate island population.

The Lombok Group separated from both the Savu and Tanimbar Groups on Function 1. The characters loading heavily (>0.5) on Function 1 were dentary length and greatest basial pit length (Table 2a). The Tanimbar Group separated from the Savu Group and partially from the Lombok Group on Function 2. The characters loading heavily (>0.5) on Function 2 were greatest basial pit length and M^2 length (Table 2).

External characters

All external characters, except snout to vent length (which showed an interaction between sex and island), were included in a DFA of these characters based on the same three groups identified above (Lombok, Savu, and Tanimbar). This DFA was also run using a reduced set of five characters (tibia length, digit 3 metacarpal length, digit 3 phalanx 1 length, digit 5 metacarpal length and ear length) and it this latter DFA that is presented here. The DFA extracted two very significant Functions. Function 1, which explained 75.5% of the variance, separated both the Savu and Tanimbar Groups from the Lombok Group (Figure 2b). The character that loaded heavily (>0.5) on Function 1 was tibia length (Table 2b). Function 2, which explained 24.5% of the variance, separated the Savu and Tanimbar Groups. The character loading heavily (>0.05) on Function 2 was digit 3 metacarpal length (Table 2b). A total of 87.9% of individuals were classified to their correct island group. Misclassifications were as follows: Two Savu Group animals to the Tanimbar Group; five Lombok Group animals to the Savu Group and 10 Lombok Group animals to the Tanimbar Group.

The Lombok, Savu and Tanimbar Groups were clearly separated in Discriminant Function space based on skull, dentary and dental characters, but less clearly so on external characters. Further, it is apparent from these plots that within these Groups there is little morphological differentiation between the islands. This is indicated by the observation that the Lombok Group cluster is defined in DF space by individuals from a single island (Lombok) and similarly the Savu Group is defined by Wetar individuals. The Yamdena and Kai Besar specimens also overlap considerably (Figure 2). In the previous study by Kitchener *et al.* (1993a) the Lombok Group represent *Taphozous m. melanopogon* and the Savu Group *T. achates*. Consequently the Wetar Island individuals classify as *T. achates*. The Tanimbar Group individuals are morphologically distinct from both these above taxa. However, the

Table 2 Standardised and unstandardised (in brackets) Canonical Variate Function coefficients for three island groupings (the Lombok, Savu and Tanimbar groups – see text) using a reduced set of five (a) skull, dentary and dental characters and (b) external characters.

Table 2a

Character	Function 1	Function 2
Dentary length	0.9925 (3.9673)	–0.0351 (–0.1404)
Basial pit length	–0.6740 (–5.1426)	0.5109 (3.8982)
Bulla length	0.4514 (–3.5766)	0.4798 (3.8009)
M^2 length	0.1256 (2.0740)	0.6495 (10.7288)
Interorbital breadth	0.3673 (1.9550)	–0.1179 (–0.6275)
Constant	–42.9653	–50.0386
Variance explained (%)	82.5	17.5

Table 2b

Character	Function 1	Function 2
Tibia length	0.8558 (0.8429)	0.1265 (0.1246)
Digit 3 metacarpal length	–0.2202 (–0.1719)	0.7704 (0.6014)
Ear length	0.4127 (0.3279)	0.2918 (0.2318)
Digit 3 phalanx 1 length	–0.4681 (–0.6943)	–0.0529 (–0.0785)
Digit 5 metacarpal length	–0.1177 (–0.0836)	0.3315 (0.2496)
Constant	0.4272	–48.8648
Variance explained (%)	75.5	24.5

DFA of all 11 islands and all skull, dentary and dental characters indicate that on Function 3 individuals from the Savu and Tanimbar Groups overlap considerably (graph not presented) indicating that individuals from the Tanimbar Group were associated in DF space with *T. achates* rather that with *T. m. melanopogon*. In the following section the populations from Tanimbar and Kai Islands are described as a new subspecies of *T. achates*.

TAXONOMY

Taphozous achates minor subsp. nov. Kitchener

Holotype

Museum Zoologicum Bogoriense (MZB) No. 15908 (field number M42899), adult male, carcase fixed in 10% formalin and preserved in 70% ethanol, skull removed, cleaned and separate, liver stored in ultrafreeze at the Western Australian Museum.

Type locality

Pulau Kelapa, 2 km W Elat, Kai Besar Island Kepulauan Kai (05°39'S, 132°59'E), mist netted from the mouth of an open well-lit cave on the beach, by D.J. Kitchener and R.A. How on 19 October 1992.

Paratypes

Yamdena Island, Kepulauan Tanimbar Desa Olilit, 1 km S Saumlaki (from a World War II Japanese made tunnel) (7°59'S, 131°22'E), 2 ♂♂ 9 ♀♀, WAM M (43527, 43529–31, 43538, 43541–43, 43547–49). 2 km S Desa Lat Dalam, (from a large 'doline' cave, among a number of other limestone caves) (7°03'S, 131°07'E), 1 ♂, WAM M 43672.

Kai Besar Island, Kepulauan Kai, beach cave, Pulau (= islet) Kelapa, 2 km W Elat, Kai Besar Island (05°39'S, 132°59'E), 4 ♂♂ 8 ♀♀, WAM M (42886–88, 42890–91, 42893–94, 42896–97, 42899–900, 42902).

Diagnosis

Taphozous achates minor differs from *T. a. achates* in averaging smaller in all characters measured (Table 1 and Kitchener *et al.* 1993: table 2)). For example, greatest skull length 20.55 (19.94–21.12) 24 *v.* 21.54 (20.91–22.55) 28; interorbital breadth 6.23 (5.82–6.62) 24 *v.* 6.48 (5.95–6.95) 28; zygomatic width 12.87 (12.42–13.19) 24 *v.* 13.22 (12.88–13.78) 26; bulla length 4.73 (4.57–4.86) 20 *v.* 4.97 (4.75–5.55) 27; greatest basial pit length 3.78 (3.49–4.07) 24 *v.* 4.04 (3.85–4.34) 28; C^1M^3 (alveoli) length 8.77 (8.45–9.12) 24 *v.* 9.23 (8.85–9.74) 28; M^2 (crown) length 1.96 (1.79–2.06) 24 *v.* 2.15 (2.07–2.28) 28; tail to vent length 26.7 (23.8–30.8) 24 *v.* 27.3 (23.4–31.6) 28; radius length 61.8 (59.5–64.1) 24 *v.* 63.8 (61.1–65.4) 28; tibia length 24.5 (23.8–25.3) 24 *v.* 25.5 (23.3–26.8) 28. Also M^2 crown length and bulla length shorter relative to least interorbital breadth (Figure 3a,b); dentary length generally shorter relative to greatest basial pit length (Figure 4); and digit 3 metacarpal length shorter relative to tibia length (Figure 5).

It differs from *Taphozous m. melanopogon* from these southern Indonesian islands by having mature adult males with a pale brown rather than a black throat beard. Most skull, dentary and dental characters average smaller. For example cranial breadth 9.63 (9.42–9.80) 24 *v.* 9.78 (9.46–10.22) 92; distance between cochleae 2.13 (2.01–2.41) 24 *v.* 2.27 (1.89–2.66) 92; bulla length 4.73 (4.57–4.86) 20 *v.* 4.97 (1.59–5.42) 91; greatest basial pit length 3.78 (3.49–4.07) 24 *v.* 4.09 (3.73–4.36) 92; radius length 61.8 (59.5–64.1) 24 *v.* 63.4 (60.9–66.1) 90. Some characters average larger. For example, least interorbital breadth 6.23 (5.82–6.62) 24 *v.* 5.99 (5.60–6.33) 92; zygomatic width 12.87 (12.42–13.19) 24 *v.* 12.60 (11.98–13.16) 92; tail to vent length 26.7 (23.8–30.8) 24 *v.* 24.6 (18.8–29.5) 90; and tibia length 24.5 (23.8–25.3) 24 *v.* 23.3 (19.9–25.5) 90. Least interorbital breadth greater relative to M^2 length

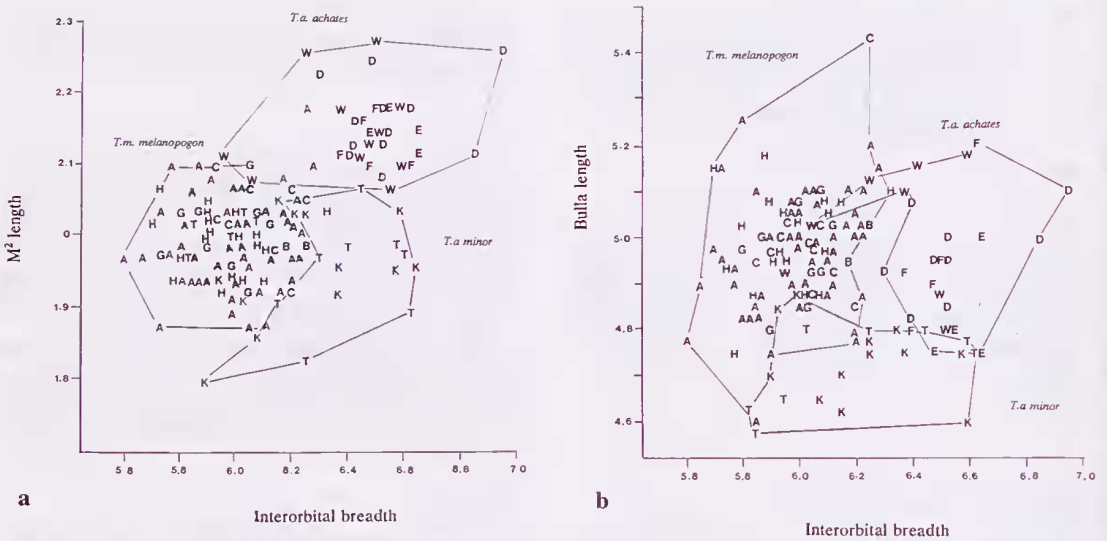

Figure 3 Plots of least interorbital breadth *versus* (a) M^2 length and (b) bulla length for both adult male and adult female *T. m. melanopogon*, *T. a. achates* and *T. a. minor* for all island populations. Codes for islands are as for Figure 2.

and bulla length (Figure 3a,b); greatest basial pit length shorter relative to dentary length (Figure 4) and tibia length generally longer relative to digit 3 metacarpal length (Figure 5).

Description

Apart from the differences mentioned in the above diagnoses *T. a. minor* is very similar morphologically and in its pelage colour to *T. a. achates*.

Distribution

Known only from Yamdena Island and Kai Besar, Maluku Tenggara, eastern Indonesia.

Etymology

The name *minor* is from the latin referring to the small size of the Yamdena and Kai Besar form of *T. achates* compared to members of the nominate subspecies.

DISCUSSION

The Bearded Tomb Bats from Tanimbar and Kai Islands are most similar to *T. a. achates* but differ in being generally smaller in most characters; some skull and external characters also differ in shape. For example, M^2 crown length, bulla length and digit 3 metacarpal length. Specimens from Wetar Island were *T. a. achates* and were not differentiated morphologically from the other known populations of this nominate subspecies on Semau, Roti, and Savu Islands. In fact these latter populations of *T. a. achates* were included within the Wetar Island population cluster in discriminant function space. This suggests that the Rotinese population had not noticeably differentiated from the nominate subspecies as suggested by Kitchener *et al.* (1993a).

Interestingly, *T. achates* occurred on Tanimbar

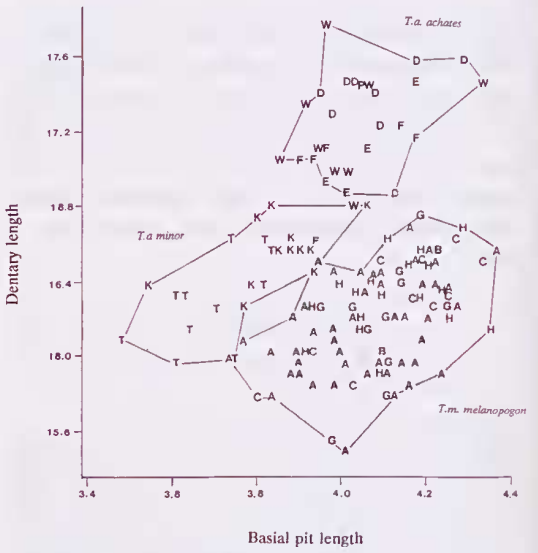

Figure 4 Plots of dentary length *versus* greatest basial pit length for both adult male and adult female *T. m. melanopogon*, *T. a. achates* and *T. a. minor* for all island populations. Codes for islands are as for Figure 2.

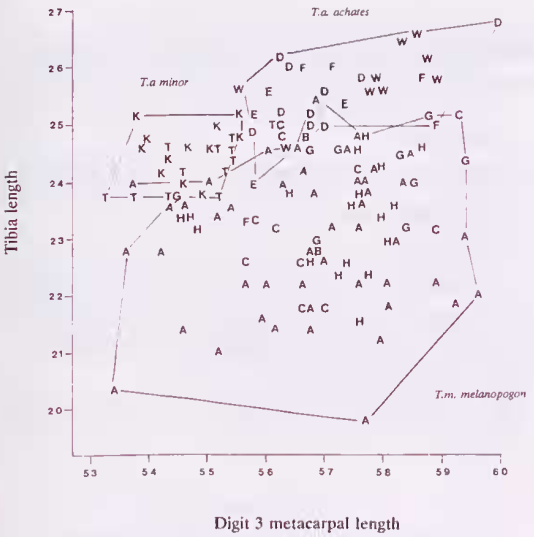

Figure 5 Plot of tibia length *versus* digit 3 metacarpal length for both adult male and adult female *T. m. melanopogon*, *T. a. achates* and *T. a. minor* for all island populations. Codes for islands are as for Figure 2.

and Kai Islands as predicted by Kitchener *et al.* (1993a). Its distribution on the islands to the immediate south and north of Timor islands add credence to its presumed presence also on Timor Island (see Kitchener *et al.* 1993a). We have not examined the specimen from Kai Island which Koopman and Gordon (1992) attributed to *T. melanopogon*, but consider that it most probably also represents *T. achates minor*.

The morphological differentiation of *T. achates* on the eastern islands of Kai and Tanimbar reflects a pattern of intraspecific differentiation observed in other mammal species in the region. For example, *Hipposideros sumbae*, *Pteropus lombocensis* and *Cynopterus nusatenggara*, all Nusa Tenggara endemics, differentiate morphologically into western and eastern forms (Kitchener and Maryanto 1993, Kitchener *et al.* 1995c,d). The bats *Hipposideros diadema*, *Nyctimene albiventer*, *N. cephalotes*, *Syconycteris australis*, *Myotis adversus*, *Rhinolophus affinis* and *R. simplex*, all species with more widespread distributions, also differentiate morphologically within this region (Kitchener *et al* 1992, Kitchener *et al.* 1993; Kitchener *et al.*; in press 1995a–d; Maharadatunkamsi 1990). This differentiation becomes more extreme on the more remote eastern islands of the Inner Arc, or on the islands of the Outer Banda Arc that have been continuously isolated by seas from other island populations. Interestingly, the House Mouse, *Mus musculus castaneus*, which is widely distributed throughout Indonesia, also differentiates into a distinct form on Wetar and Kisar Islands (Kitchener, unpublished data).

Other specimens examined

Taphozous achates achates

Desa Ipokil, Wetar Island, Nusa Tenggara Timur (7°50'S, 126°16'E), 4 ♂♂ 5 ♀♀ WAM M(44510, 44520–27).

ACKNOWLEDGEMENTS

We are grateful for the support of Mr A. Reeves, Director, Western Australian Museum and to Dr Soetikno, Director, Puslitbang Biologi, and Mr M. Amir, Director, Balitbang Zoologi, Bogor Indonesia and the Directors of Sub Balai Konservasi in Nusa Tenggara Barat (Ir. P. Supriadi), Nusa Tenggara Timur (Ir. J. Mochtar) and Maluku Tenggara (Ir. J. Rustandi).

A number of colleagues assisted in the field work of whom Dr R.A. How, Mr R.E. Johnstone, Western Australian Museum, and Ir. Maharadatunkamsi and Ir. I. Maryanto, Balitbang Zoologi, were principal. Mr C. Keast, Western Australian Museum, assisted in the preparation of skulls for this study. Mrs S. Dalton, Western Australian Museum, typed the manuscript.

The field work was supported by a number of grants, including National Geographic Society Research Grants, Washington and the Australian Nature Conservation Agency, Canberra. Freight costs were subsidised by Garuda Airlines.

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Manuscript received 25 May 1994; accepted 13 February 1995.